

Spatial and temporal patterns of amphibian species richness on Tianping Mountain, Hunan Province, China

DEAR EDITOR,

Exploring species richness patterns across space and time can help in understanding species distribution and in formulating conservation strategies. Among taxa, amphibians are of utmost importance as they are highly sensitive to environmental changes due to their unique life histories (Zhong et al., 2018). Here, we investigated the spatial and temporal patterns of amphibian species richness on Tianping Mountain in China. Specifically, we established 10 transects at low to high elevations, and sampled amphibians in April, June, August, and October 2017. Our results demonstrated that amphibian species composition and richness varied significantly at both spatial and temporal scales and were associated with gradients of environmental change in microhabitats on Tianping Mountain.

Biodiversity is a hot topic in community ecological research and exhibits a strong relationship with ecosystem functioning (Wang & Brose, 2018; Zhao et al., 2018). Although biodiversity consists of multiple components, species richness is a fundamental measurement underlying various ecological concepts and models (Gotelli & Colwell, 2011). Exploring species richness patterns across space and time can help to understand the distribution of organisms (Fu et al., 2006), reveal the mechanism of species coexistence (Hu et al., 2011), formulate conservation strategies (Olds et al., 2016), and assess environmental changes (Butchart et al., 2010).

Spatial patterns of species richness are usually tested along altitudinal or latitudinal gradients at the local and regional scales, respectively. At the local scale, species richness typically exhibits two types of response along elevational gradients; i.e., it decreases continuously or displays a hump-shaped relationship with increasing elevation (Rahbek, 1995, 2004). These relationships can be explained by environmental factors such as climate, area, and habitat heterogeneity (Cruz-

Elizalde et al., 2016; Hernández-Salinas & Ramírez-Bautista, 2012; McCain, 2009; Rahbek, 1995; Sanders et al., 2003) or can be attributed to mid-domain effects, with increasing species distribution overlap towards the center of a bounded geographic domain free of environmental gradients (Colwell et al., 2004; Wu et al., 2013a). At the larger geographic scale (e.g., latitudinal gradients), species richness can increase from the poles to the tropics (e.g., global data of amphibians, birds, and mammals; Marin & Hedges, 2016). This is likely because tropical areas have greater historical lineages and higher environmental heterogeneity than temperate zones (Jansson et al., 2013; Stevens, 2011). In contrast, marine species richness along latitudinal gradients (for both vertebrates and invertebrates, and all species together) is bimodal, with a dip in richness occurring at the equator (Chaudhary et al., 2017). This relationship is strongly determined by temperature, which can influence animal biology and productivity within ecosystems (Chaudhary et al., 2017).

Temporal environmental fluctuations (e.g., seasonality) can also control species composition and richness (Tonkin et al., 2017). The unique assemblages observed at specific times of the year depend on the ecological conditions of each season (Chesson, 2000), and have been well documented in different fauna. For instance, temporal changes in bird species richness can be attributed to seasonal migration (Somveille et al., 2015). In terms of fish communities, species richness and assemblages can vary seasonally due to minimization of interspecific competition for resources (Shimadzu et al., 2013). Therefore, exploring temporal (seasonal) patterns of species richness can help to understand species coexistence and ecosystem stability (Thibaut & Connolly, 2013).

Although numerous studies have examined spatial (e.g.,

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Acharya et al. 2011; Bhattarai et al., 2004; Fu et al., 2007; Gojo Cruz et al., 2018; Kraft et al., 2011; Khatiwada et al., 2019; Wu et al., 2013a, 2013b) and temporal patterns (e.g., Bender et al., 2017; Shimadzu et al., 2013; Tonkin et al., 2017) of species richness in different taxa separately, empirical studies are still needed for simultaneous quantification. This is because both space and time can affect the distribution and activities of species at the local scale. For instance, species belonging to different spatial guilds may exploit different habitat types. Population size may increase at different times as species can adapt to changes in temporal environmental conditions over their life cycle (Shimadzu et al., 2013). This is especially true for amphibians due to their restricted distribution ranges as well as their seasonal migration for spawning and after metamorphosis (Fei et al., 2009). Therefore, in the present study, we focused on the spatial and temporal (seasonal) changes in species richness in amphibians distributed on Tianping Mountain, China. Specifically, we (1) revealed the amphibian species assemblages along elevational gradients, as well as those in different seasons, (2) explored the environmental factors that determined species composition, and (3) tested the spatial and temporal patterns of species richness. Methodological details are provided in the Supplementary Materials.

In total, 15 species belonging to seven families were recorded during the four sampling sessions (Supplementary Table S1). Results showed that amphibian assemblages changed along the elevational gradients. Overall, the dominant species recorded at the low, mid-, and high elevation transects included *Amolops ricketti* and *Odorrana schmackeri*, *Paramegophrys liui*, and *Paa boulengeri* and *Leptobrachium boringii*, respectively (Figure 1A). The amphibian assemblages also exhibited strong temporal shifts during the four seasons. The dominant species in April, June, August, and October were *Paramegophrys liui* and *L. boringii*, *Megophrys sangzhiensis* and *Pseudohynobius flavomaculatus*, *O. margaretae* and *O. schmackeri*, and *Paa boulengeri* and *A. ricketti*, respectively (Figure 1B).

The redundancy analysis (RDA) results were significant when testing the effects of environmental factors on amphibian species composition ($P=0.005$). The first two axes explained 31.73% of the variation (20.13% and 11.60%, respectively). Among the 16 environmental factors, air humidity, water temperature, altitude, tree number, canopy density, shrub coverage, fallen leaf coverage, fallen leaf depth, and water conductivity had significant effects on species composition ($P<0.05$). Juvenile and adult *O. schmackeri*, adult *A. chunganensis*, juvenile and adult *A. ricketti*, and adult *Fejervarya multistriata* were positively associated with water temperature and water conductivity, but were negatively associated with altitude, tree number, canopy density, and fallen leaf depth. In contrast, juvenile *Bufo gargarizans*, adult *L. boringii*, and adult *Paramegophrys liui* were positively associated with altitude, tree number, canopy density, and fallen leaf depth, but were negatively correlated with water temperature and water conductivity. In addition,

adult *Feirana quadranus*, adult *Pseudorana sangzhiensis*, adult *O. margaretae*, juvenile and adult *Paa boulengeri*, adult *M. sangzhiensis*, and adult *Rhacophorus chenfui* were positively associated with shrub coverage and air humidity. In contrast, adult *Hyla gongshanensis* and juvenile *Pseudohynobius flavomaculatus* were negatively associated with shrub coverage and air humidity (Figure 1C).

Overall, total amphibian species richness increased significantly along elevational gradients when incorporating data from all four sampling sessions ($R^2=0.53$, $P=0.010$; Figure 1D), indicating that more species were detected at high elevation sites. However, the response of species richness to elevational gradients differed each month. Specifically, there were no significant changes in April and August ($R^2=-0.12$, $P=0.844$; $R^2=-0.06$, $P=0.519$), but a significant increase and U-shaped relationship were observed in June and October, respectively ($R^2=0.38$, $P=0.034$; $R^2=0.70$, linear term: $P=0.009$, quadratic term: $P=0.014$; Figure 1E). At the temporal scale, total species richness varied significantly among the different months (Friedman test; $\chi^2=16.129$, $df=3$, $P=0.001$). Specifically, species richness in April was significantly lower than that in August ($W=17$, $P=0.011$), but was significantly higher than that in October ($W=76$, $P=0.044$). Species richness in October was significantly lower than that in June ($W=93$, $P=0.001$) and August ($W=97$, $P<0.001$). However, there was no significant difference in species richness between April and June ($W=24.5$, $P=0.052$) or between June and August ($W=43$, $P=0.612$; Figure 1F).

Overall, our results indicated that amphibian species assemblages varied along elevational gradients. Specifically, *A. ricketti* and *O. schmackeri* were the dominant species at the low elevation transects. However, these species, as well as *F. multistriata* and *H. gongshanensis*, were restricted to transects below 800 m a.s.l. (i.e., were not recorded at mid- or high elevations). Results also showed that *Paramegophrys liui* was dominant at the mid-elevation transects, whereas *Paa boulengeri* and *L. boringii* were dominant at the high elevation transects. In addition, we found one high elevation-restricted species (*Pseudorana sangzhiensis*). These results support previous claims that elevations associated with specific habitat conditions (e.g., temperature and vegetation variation) are important for determining amphibian species distribution (Khatiwada et al., 2019; Meza-Joya & Torres, 2016) and provide specific spatial niches for species. We also found that temporal niche utilization differed among the amphibians, with dominant species changing from *Paramegophrys liui* and *L. boringii* in April, to *Pseudohynobius flavomaculatus* in June, *O. schmackeri* in August, and *Paa boulengeri* and *A. ricketti* in October. Some species were also seasonally restricted. For instance, *Paramegophrys liui* was not detected after June, *O. schmackeri* and *M. sangzhiensis* were only active in June and August, and *Pseudorana sangzhiensis* was only recorded in August. These results could be attributed to breeding times and temperature adaptations (Fei et al., 2009; Snyder & Weathers, 1975). Therefore, our results are in agreement with previous studies, which state that *Paramegophrys liui* and *L.*

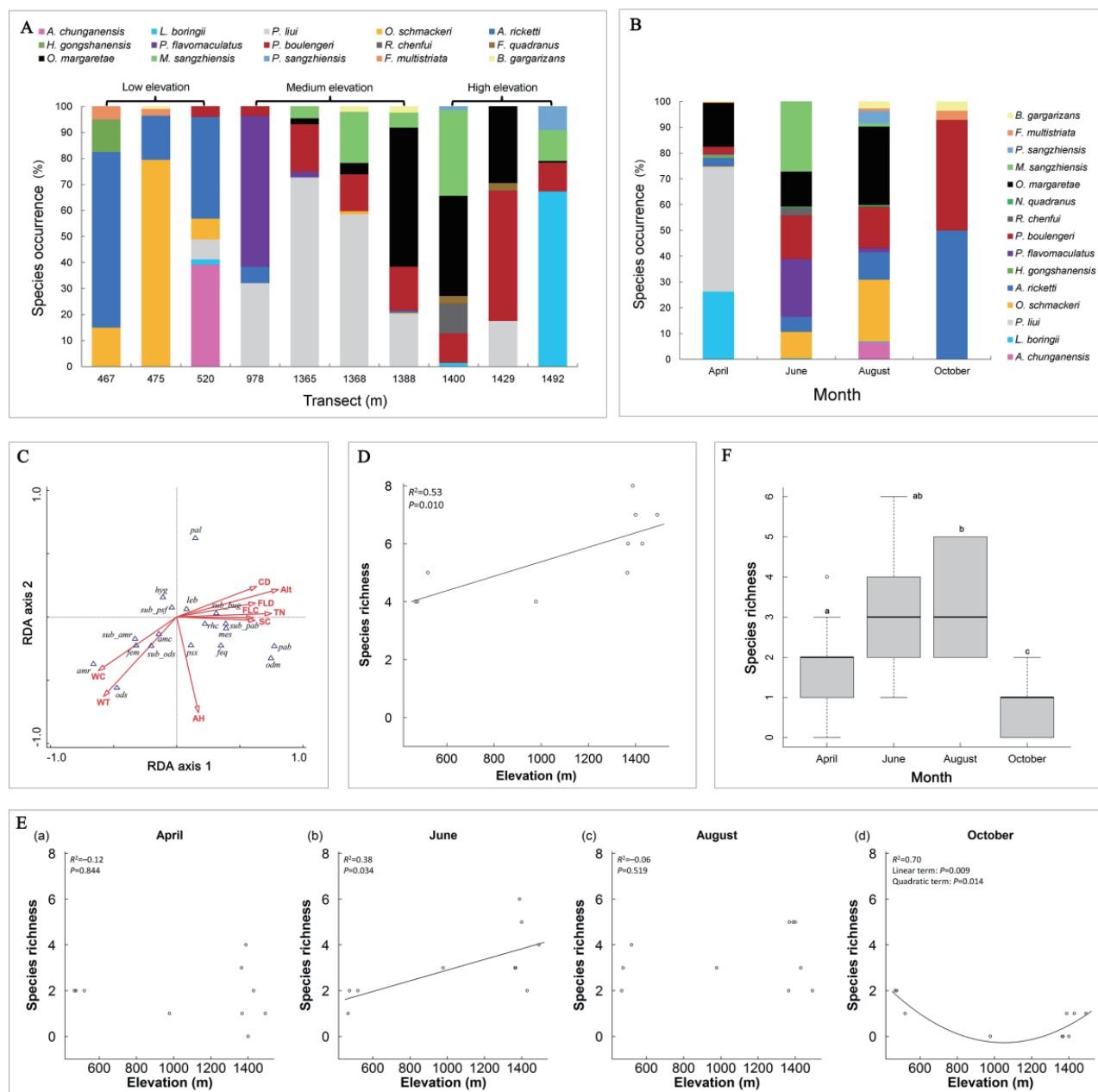


Figure 1 Spatial and temporal patterns of amphibian species richness on Tianping Mountain.

A: Species occurrence (percentage of individuals) in different sampling transects. B: Species occurrence (percentage of individuals) in different months. C: Redundancy analysis (RDA) of relationships among environmental factors and amphibian species composition. Length of environmental vector indicates degree of correlation. Only significant variables ($P < 0.05$) are depicted. Abbreviations of environmental factors and amphibian species are listed in Supplementary Table S1 and Table S2, respectively. D: Relationship between total amphibian species richness and elevation. E: Relationship between amphibian species richness and elevation each month. F: Temporal changes in amphibian species richness over four months. Different letters on top of error bars indicate significant difference between pairwise months ($P < 0.05$).

boringii breed in April–July and February–April, respectively (Fei et al., 2009, 2012), whereas *O. schmackeri* and *M. sangzhiensis* usually breed in June–August (Fei et al., 2009, 2012). We also sampled several species in all seasons (e.g.,

Paa boulengeri and *A. ricketti*), which may be related to their broader temperature adaptation range (Fei et al., 2009, 2012).

Previous studies have indicated that *Paramegophrys liui* and *L. boringii* usually require high elevation habitats with

broad vegetation coverage (Fei et al., 2009, 2012), which provide good breeding sites. This may explain why their abundance was positively correlated with environmental factors such as canopy density, fallen leaf depth, and tree number. However, their abundance was negatively correlated with water temperature as their breeding season occurs from March to June under relatively low temperatures (Fei et al., 2012; Yu & Lu, 2010). Juvenile *B. gargarizans* exhibited similar patterns as *P. liui* and *L. boringii*, which was probably because they recently underwent metamorphosis from water bodies. However, *A. chunganensis*, *A. ricketti*, and *O. schmackeri* were negatively associated with altitude, as these species prefer large, strong-flowing streams with low vegetation cover, which were more common at the lower elevation transects with higher temperatures (Wu et al., 2015; Xiong et al., 2005). The observations for *F. multistriata* at low elevations could be attributed to their high abundance in and preference for lowland paddy fields close to large streams. Unsurprisingly, *F. quadranus*, *Pseudorana sangzhiensis*, *O. margaretae*, *Paa boulengeri*, *M. sangzhiensis*, and *R. chenfu* were positively associated with shrub coverage and air humidity, as these conditions provide diverse food items such as insects, snails, and crabs (Huang et al., 2011; Yuan & Wen, 1990). In contrast, *H. gongshanensis* and juvenile *Pseudohynobius flavomaculatus* were negatively correlated with air humidity and shrub coverage as they inhabit paddy fields close to streams (Liao & Lu, 2010) and small ponds covered by rocks (Fei et al., 2009), respectively.

In contrast with many earlier studies (e.g., Hu et al., 2011; Khatiwada et al., 2019), total amphibian species richness increased continuously along the elevational gradients, with more species detected at higher elevations. This observation is interesting as most previous studies suggest that amphibian species richness should exhibit a hump-shaped response to elevation due to mid-domain effects (e.g., amphibians in Hengduan Mountain, China; Fu et al., 2006; amphibians in tropical Andes; Meza-Joya & Torres, 2016) or decrease continuously with elevation (e.g., eastern Nepal Himalaya; Khatiwada et al., 2019). This is because high elevations (e.g., >3 000 m on Hengduan Mountains and eastern Nepal Himalaya; Hu et al., 2011; Khatiwada et al., 2019) usually correspond to low temperatures, with fewer amphibian species able to survive in cold regions (Funk et al., 2012). Our conflicting results could be attributed to the limited elevation of transects selected on Tianping Mountain (<1 500 m), with temperature not a primary limiting factor of amphibian species richness at the spatial scale. In addition, our results could also be attributed to the larger heterogeneity of habitats at higher elevations on Tianping Mountain (Cao et al., 1997), which could support more amphibian species (Hernández-Salinas & Ramírez-Bautista, 2012; Meza-Joya & Torres, 2016). It was not surprising that more species were observed in June and August as these months occur in the active season (warmer and wetter climate conditions) for most amphibian species, with their populations increasing in suitable habitats (Bickford et al., 2010).

In conclusion, the present study demonstrated the spatial and temporal patterns of amphibian species richness on Tianping Mountain in Hunan Province, China. Future studies should focus on more facets of biodiversity to better understand the roles of spatial and temporal variation in community assembly processes of mountain-dwelling amphibians. As the spatial and temporal niches of amphibian species were different, specific conservation strategies should be implemented. Furthermore, we confirmed that amphibian species occurrence was strongly determined by biotic and abiotic features of their microhabitats, which mediated species composition along the elevational transects. Because microhabitats are easily affected by human disturbance, long-term monitoring should be conducted to investigate the relationship between amphibian diversity and environmental change.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Field sampling was approved by the Management Office of the Badagongshan Nature Reserve (No. BDGSNR201204002). Animals collection and measurement protocols were approved by the Animal Care and Use Committee of Chengdu Institute of Biology (No. CIB2010031015).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

T.Z. and J.P.J. conceived and designed the study. W.B.Z., C.L.Z., C.L.L., B.Z., D.X., and T.Z. collected the data. W.B.Z. and T.Z. analyzed the data and wrote the first draft of the manuscript. C.L.Z., W.Z., and J.P.J. commented on the manuscript. All authors read and approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

SUPPLEMENTARY MATERIAL AND METHODS

Study area

The present study was conducted on the Tianping Mountain, the core region of Badagongshan National Nature Reserves, which is located in northwest Hunan Province, China (N29.714072°–29.787100°, E109.906154°–110.170800°). The elevational gradients are from 300 to 1 890 m, covering three distinct climatic zones. Specifically, the low elevation area (<800 m) is warm, with the mean annual temperature ranging from 13.7 to 15.9 °C. This is the hilly agriculture-forestry zone, where the vegetation is dominated by crops and evergreen broad-leaved forest. The mean annual temperature of medium elevation area (800–1 400 m) is 12.2–13.7 °C, which corresponds to evergreen broadleaf forest zone. The high elevation area (1 400–1 890 m) is composed of evergreen deciduous broadleaf forest, which has strong wind, heavy rain, and heavy snow during winter, and the mean annual temperature is below 10.0 °C (Xiong et al., 1999).

Amphibians sampling

Ten transects (200 m×2 m) were randomly selected from low to high elevational gradients (Figure S1), which located along stream tributaries. These transects were separated from each other by a deep mountain gorge and/or streams to reduce the spatial autocorrelation, with more than 1.5 km of the pairwise distance existing between them. Amphibian communities sampling were conducted in April, June, August, and October in 2017, separately. These four times sampling events were corresponded with distinct seasons (i.e., spring, early summer, midsummer, and autumn), covering the breeding, foraging, and migration seasons of amphibians. We used the combination of distance sampling and quadrat sampling methods following Zhao et al. (2018) and Khatiwada et al. (2019), which has been proved effectively to sample the combination of anurans and stream amphibians (e.g., salamanders, Funk et al., 2003; Dodd, 2010). All of the captured individuals were identified to species, determined to developmental stages (adult or juvenile), measured for snout-vent length to the nearest mm, weighted, photographed, toe-clipped (molecular identification was used if individuals cannot be identified based on morphological traits), and then released back to the sites from which they were captured.

Environmental factors

A set of 16 environmental factors associating with biotic and abiotic features of amphibians microhabitat were select based on previous studies demonstrating that they can potentially play important roles in shaping amphibian assemblages (Grundel et al., 2015; Keller et al., 2009; Khatiwada et al., 2019; Wyman, 1988; Wyman & Jancola, 1992). Details of the environmental factors and the related methodologies that used to collect them were as follows: air temperate was measured using a mercury thermometer. Air humidity was measured by a digital humidity meter (Peakmeter MS6508). Altitude was recorded by using a GPS (ICEGPS 660). Water depth, water width, fallen leaf depth were measured five times within 20m in each transect by using a steel tape, and the average values were used to do the analyses. Canopy cover (%) of the vegetation was measured following Lemmon (1957) by using a spherical densitometer, with five locations were selected and four directions (N, S, E, W) were measured in each location, and we also used the

average values to do the analyses. Tree number was recorded in each transect (i.e., all of the trees located in the 200 m×2 m transect). Shrub coverage, fallen leaf coverage, and rock coverage were averaged by five locations data, with each location was estimated by the same person. Soil pH was recorded using a soil pH Meter (ZD-05, Zhengda, China). Water temperature, water pH, and conductivity were measured by using a portable fluorescence photometer (Orion, Thermo Fisher Scientific, USA). Water velocity was recorded five times using a velocimeter (Xianguide, LS1206B, China) in each transect, and the average value was used for subsequent analyses. In total, all of the environmental factors in each transect were measured four times (i.e., at April, June, August, and October, respectively; Table S2).

Statistical analyses

We first performed a detrended correspondence analysis (DCA; Hill & Gauch, 1980) to determine whether redundancy analysis (RDA) or canonical correspondence analysis (CCA) would be the most appropriate model to describe the association between amphibian species composition (i.e., life stages level) and environmental factors. The DCA ordination gradient was 1.12 SD, suggesting that the linear model associated with RDA was the appropriate model to describe the association between amphibian species composition and environmental factors (ter Braak, 1986). The importance of each environment factor in the biplot was indicated by the length and angle of the vectors. We subsequently used Monte Carlo permutation test with 999 permutations to test whether environment factors significantly explained amphibian assemblages data. A forward selection procedure with 999 permutations was used to test the contributions of each environmental factor on all axes conjointly (Zhao et al., 2016). Species richness was represented by the number of species. The response of amphibian species richness to elevational gradients (spatial variation) was tested using linear regressions. Since the relationship may be either non-monotonic (U shape and hump-shape) or monotonic (linear), a quadratic term was included in the models that were subsequently retained only if significant ($P < 0.05$; Crawley, 2007). Finally, we conducted a Friedman test with a Wilcoxon rank sum test to compare the potential differences of amphibian species richness between four months (i.e., seasons). All statistical analyses were conducted in R 3.60 (R Development Core Team, 2011).

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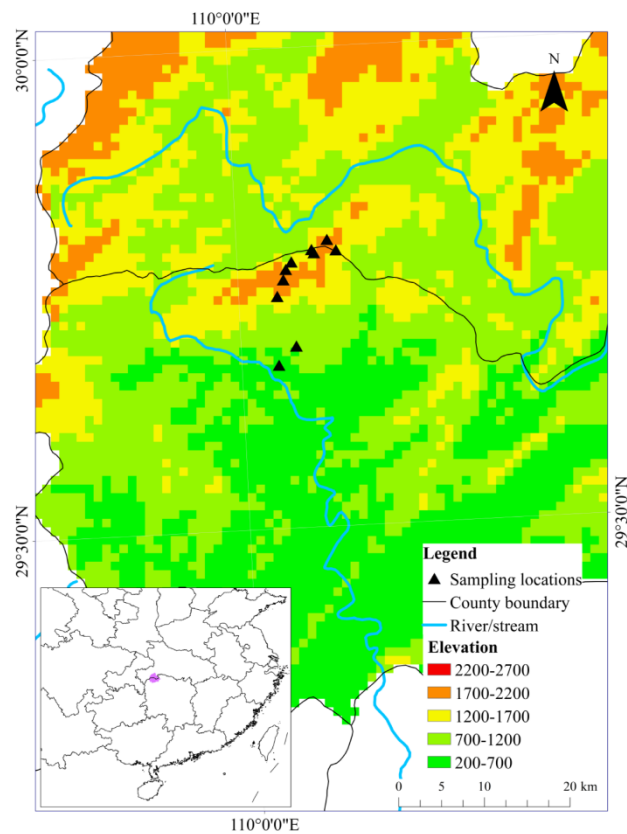
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Supplementary Table S1 Species (and the abbreviation) that were captured on the Tianping Mountain

Oder	Family	Species	Abbreviation
Anura	Bufonidae	<i>Bufo gargarizans</i>	bug
		<i>Amolops chunganensis</i>	amc
	Ranidae	<i>Amolops ricketti</i>	amr
		<i>Odorrana margaretae</i>	odm
		<i>Odorrana schmackeri</i>	ods
		<i>Pseudorana sangzhiensis</i>	pss
		<i>Fejervarya multistriata</i>	fem
	Dicroglossidae	<i>Feirana quadranus</i>	naq
		<i>Paa boulengeri</i>	pab
		<i>Rhacophorus chenfui</i>	rhc
	Hylidae	<i>Hyla gongshanensis</i>	hya
	Megophryidae	<i>Paramegophrys liui</i>	pal
		<i>Leptobrachium boringii</i>	leb
		<i>Megophrys sangzhiensis</i>	mes
Caudata	Hynobiidae	<i>Pseudohynobius flavomaculatus</i>	psf

Supplementary Table S2 Environmental factors (name and abbreviation) measured in each transect

Name	Abbreviation	Range	Mean (<i>SD</i>)
Air temperate (°C)	AT	9.17–25.13	17.82(4.41)
Air humidity (%)	AH	55.03–99.53	80.65(12.08)
Water temperate (°C)	AT	10.00–21.47	14.27(2.86)
pH-water	WpH	6.27–7.12	6.59(0.23)
Altitude (m)	Alt	467–1492	1 084(428)
Water depth (mm)	WD	10.30–93.33	36.38(25.71)
Water width (m)	WW	1.57–20.00	5.85(5.51)
Tree number	TN	0–204	67(72)
Canopy density (%)	CD	0–80.83	37.08(34.29)
Shrub coverage (%)	SC	0–46.88	16.70(14.74)
Fallen leaf coverage (%)	FLC	0–15.00	4.82(5.29)
Fallen leaf depth (mm)	FLD	0–3.60	1.35(1.36)
Rock coverage (%)	RC	2.50–100.00	29.96(25.42)
Flow rate (cm/s)	FR	13.92–47.16	24.87(9.15)
pH-soil	SpH	6.27–7.00	6.63(0.19)
Water conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	WC	16.49–294.67	103.38(85.88)



Supplementary Figure S1 Map of the study area showing the Tianping Mountain, China
The triangles denote transects used in the present study to survey amphibians.